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THE GENERA OF CRASSULACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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CRASSULACEAE A. P. de Candolle in Lamarck & De Candolle, Fl. Franç. ed. 3. 4(1): 382. 1805, nom. cons.

(STONECROP OR ORPINE FAMILY)

Annual, biennial, or [monocarpic or] polycarpic perennials, the plants mostly succulent, often evergreen, herbs, subshrubs [or shrubs, many of treelike habit, or rarely scandent], usually terrestrial from fibrous roots, sometimes developing fleshy or woody caudices or rhizomes [or rarely epiphytic]. Leaves exstipulate, alternate, opposite, or whorled, the internodes sometimes reduced and the plants rosulate, the blades simple or occasionally pinnately compound, usually fleshy and succulent, cylindrical to flattened with entire to crenate or dentate margins, the leaves of vegetative and flowering shoots often dissimilar; vegetative reproduction commonly by bulbil or plantlet production in the crenations of the leaves or by meristematic activity in detached leaves or stems. Flowers perfect or

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imperfect (the plants then dioecious or polygamodioecious), actinomorphic, usually proterandrous, arranged in terminal or axillary, usually bracteate corymbose, helicoid, or scorpioid cymes, panicles, simple to compound dichasia, or solitary [or clustered] in the axils of leaves [or rarely in spikes]; insertion of the sepals and petals hypogynous. Sepals (3) 4 or 5 [or up to 30], free or connate and then forming a calyx tube. Petals the same number as the sepals, free or occasionally connate, forming a tubular to urceolate, usually ribbed corolla tube. Stamens as many or twice as many (and then obdiplostemonous) as the sepals, insertion hypogynous or epipetalous, free [or occasionally the filaments basally connate]; anthers basifixed, dehiscing introrsely by longitudinal slits, 4-sporangiate (2-loculate at anthesis), with a secretory tapetum; pollen 2-celled when shed (as monads), 3-colporate. Gynoecium apocarpous or basally syncarpous, the carpels usually the same number as the sepals, sessile or stipitate, tapering gradually or abruptly into erect or divergent styles, the styles terminated by small, often poorly differentiated apical or subapical stigmas; each carpel subtended by a scalelike [rarely petaloid] nectariferous gland [or rarely, the gland absent]; ovary 1-loculate, superior, with numerous [rarely few to solitary] anatropous, crassinucellar, bitegmic ovules on a parietal or marginal placenta. Fruit a follicle or follicetum of several basally connate follicles, the follicles dehiscent along their adaxial sutures or rarely by abaxial flaplike valves; seeds usually numerous, small, rarely winged; embryo small, straight, embedded in scant, fleshy, cellular endosperm [or endosperm occasionally lacking]; megagametophyte of the Polygonum or (rarely) Allium type; embryogeny of the Caryophyllad type. (Sedaceae Necker, nom. subnud.) TYPE GENUS: *Crassula* L.

Upward of 1500 species in as many as thirty-five genera and six generally recognizable subfamilies, distributed throughout the world, primarily in areas of subtropical climate with alternating wet and dry seasons. Great concentrations of species and genera occur in southern Africa, Madagascar, the Canary Islands, southern Asia, Mexico, and the Mediterranean region. The family is poorly represented in Australia (one genus), Oceania (two genera) and South America. Nine or ten species in three genera (representing two subfamilies) are indigenous in the southeastern United States, while eleven or twelve additional species (eight of which represent a fourth genus and a third subfamily) have escaped from cultivation and have become naturalized in this area.

While the family Crassulaceae has generally been conceded to form a natural, well-defined taxon, agreement with regard to the definition of taxa at essentially all subordinate levels has been fraught with difficulties, and there is no general consensus as to the number of species, genera, or subfamilies. Berger (1930), who treated the entire family, recognized six subfamilies that, except for inevitable intermediate taxa, are fairly well defined morphologically, if not biologically. Baldwin (1939) suggested that the relationships within the family are interlinear as well as linear, and Berger (1930, p. 382) cautioned about the use of technical characters in the definition of taxa. Berger's sentiments were reiterated by Moran (1942b), who said that "if too much emphasis were placed on technical characters, the numerous exceptions and intergradations would necessitate the combination of genera until but six or only one genus remained."

The characters that have been used to define subfamilies are largely concerned with the number of floral parts and the connation of the petals, as well as the position of the flowering shoots and the arrangement of the leaves. Certainly some of the problems below the level of subfamily are due to the usual succulence of the plants and the poor specimens that result from attempts to press the plants by conventional herbarium techniques. It is almost imperative that studies of the Crassulaceae be made with living plants or at least with fluid-preserved materials.

Members of the family are generally succulent and usually show a whole series of xeromorphic adaptations (including anatomical and physiological changes), as well as adaptations in the life cycles of some species (e.g., *Diamorpha Smallii*) for drought evasion. Most species have an abundance of water storage tissue in the leaves (in which a palisade layer is rarely or poorly differentiated) and in the stems (where the parenchymatous or collenchymatous tissues of the cortex and pith are well developed). Vascular tissue is unevenly and irregularly distributed throughout the storage tissues, the phloem is poorly developed, and the xylem of the stems is generally in a continuous cylinder.

While trichomes are uncommon in the family, the hairs (as well as the adventitious roots and epidermal cells) of some species are suspected of absorbing water directly from the atmosphere. A waxy coating secreted by the epidermis is characteristic of the leaves, and hydathodes are relatively common, often being distributed over both surfaces of the leaves and visible to the naked eye as small pits. The stomata, which are usually surrounded by three subsidiary cells, are likewise usually well distributed over both surfaces of the leaves.

The stomata of some investigated species are open primarily at night and closed during the day, a phenomenon that coincides with carbohydrate decrease, excessive increase in malic acid content, and water-vapor loss at night, and with starch accumulation and reduced acidity during the daylight hours. Carbon fixation occurs in the leaves at night when the stomata are open, and is thus temporally separated from the light reactions in the photosynthetic process. During the day, when the stomata are closed and water loss is thus reduced, the fixed carbon is reduced to carbohydrate. This physiological syndrome, known as crassulacean acid metabolism (CAM), along with the Calvin-Benson cycle (C_3 plants) and the C_4 decarboxylic pathway (C_4 plants), is one of three distinct carbon fixation and reduction mechanisms known in vascular plants. While the CAM pathway was originally described from crassulaceous plants, it is not restricted to them, and it may be facultative, depending upon environmental conditions. Kluge (1977) has found that under normal conditions in nature, *Sedum acre* is a C_3 plant, but that under experimental water stress, carbon dioxide exchange shifts from the Calvin cycle to CAM. As indicated by Black & Williams (1976), all CAM plants are succulents, but not all succulents are CAM plants. Apparently there is little if any taxonomic significance to CAM, since the pathway has been reported for members of four monocotyledonous and thirteen dicotyledonous families, as well as for a fern, *Drymoglossum piloselloides*. While only the outlines of the process are given above, there has been much research on CAM; for further information, see the papers listed under family references, as well as a few titles included under *Kalanchoë*.

Other features of the Crassulaceae of biological interest are the wide range of chromosome numbers (from $2n = 8$ to $2n =$ ca. 500) and the occurrence of considerable and widespread intraspecific variation in chromosome number, including both polyploidy and aneuploidy. Uhl (1970) reports that two species of *Graptopetalum* Rose have gametic chromosome numbers of $n = 245 \pm 5$ and $n = 270 \pm 5$, higher counts than have been reported for any other seed plants. The occurrence of heteroploidy has proved to be confusing, particularly with regard to species delimitation, and especially when few if any morphological characters correlate with the different chromosome numbers.

Uhl (1976) has determined that the majority of the Crassulaceae of Mexico (subfams. Sedoideae and Echeverioideae) ". . . belong to a giant biosystematic comparium, since they have been interconnected, directly or indirectly, by artificial hybrids. More than 1100 different hybrids have been produced among at least 165 species of the genera *Echeveria*, *Sedum*, *Pachyphytum*, *Graptopetalum*, *Thompsonella*, *Villadia*, and *Lenophyllum* . . . ." Moreover, the intersubfamilial hybrid between *Echeveria linguifolia* Lemaire and *Sedum cremnophila* Clausen, both with $2n = 66$, has normal meiosis and 95 percent normal pollen (Uhl, 1966, 1976). It would appear that continued chromosome studies, together with hybridization programs, in other groups of the family will alter the concept of relationships at almost all ranks and will undoubtedly provide the basis for a more acceptable (if not a more utilitarian) taxonomy.

In current systems of classification, the Crassulaceae are closely allied with the Saxifragaceae, from which they can be distinguished by their usual succulence and their flowers with the number of petals or sepals and carpels the same, the carpels subtended by nectariferous glandular scales, and the seeds lacking (or with only scant) endosperm. *Penthorum* L. is the only genus that has created problems in the delimitation of the Crassulaceae, and Quimby (1971) has concluded that this family is a natural assemblage only if *Penthorum* is excluded. Although *Penthorum* exhibits characters that are in many respects intermediate between the two families (it has occasionally been placed in its own monogeneric family, Penthoraceae Rydb. ex Britton), in this flora *Penthorum* has been included in the Saxifragaceae in subfam. Penthoroideae Engler, for the reasons outlined there (Spongberg, 1972, p. 421).

Thorne (1968) and Cronquist (1968) include Crassulaceae and Saxifragaceae in the Rosales, while Takhtajan (1969) includes the two families in the Saxifragales. Both Takhtajan and Cronquist note that the Podostemales (Podostemaceae) (included in the Rosales by Thorne) are undoubtedly derived from the Crassulaceae. Support for a close relationship between the Crassulaceae and the Podostemaceae, seemingly dissociative taxa, comes primarily from embryological similarities noted by Mauritzon (1939), Maheshwari (1945), and Subramanyam (1962) that have been summarized in this flora by Graham & Wood (1975). An evolutionary trend toward adaptation to an aquatic habitat is also evident in the Crassulaceae in some members of *Crassula* sect. TILLAEOIDEAE.

None of the Crassulaceae is of great economic importance, although many of the species are cultivated as ornamentals, both as pot plants and as garden perennials. In our area, species of *Sedum* and *Sempervivum* (subfam. Sempervivoideae Berger) are commonly grown in rock gardens and on walls. Some of the species have been used in folk medicine and as greens in salads.

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KEY TO THE GENERA OF CRASSULACEAE IN THE SOUTHEASTERN UNITED STATES

A. Petals (3) 4 or 5, free or only slightly connate at base; stamens free from the petals and inserted hypogynously.
  B. Stamens 2× the number of sepals and petals (subfam. Sedoideae).
    C. Gynoecium apocarpous; flowers perfect or imperfect, 4- or 5-merous; mature follicles dehiscing longitudinally; annuals, biennials, or perennials. .... 1. *Sedum.*
    C. Gynoecium syncarpous at base; flowers perfect, 4-merous; mature follicles dehiscing by a tear-shaped, flaplike, abaxial valve; winter annuals. .... 2. *Diamorpha.*
  B. Stamens the same number, (3) 4, as the sepals and petals; gynoecium apocarpous; mature follicles dehiscing longitudinally along the adaxial suture; annuals or biennials (subfam. Crassuloideae). .... 3. *Crassula.*
A. Petals 4, connate; stamens 8 (in 2 whorls of 4), epipetalous; gynoecium basally syncarpous; perennials naturalized in southern Florida (subfam. Kalanchoideae). .... 4. *Kalanchoë.*

Subfam. SEDOIDEAE Berger

1. **Sedum** Linnaeus, Sp. Pl. 1: 430. 1753; Gen. Pl. ed. 5. 197. 1754.

Annual, biennial, or perennial, ± succulent, often evergreen or deciduous herbs [subshrubs or shrubs], cespitose or with mat-forming vegetative shoots and then usually with slender, ascending or erect, terminal or occasionally axillary flowering stems. Roots generally fibrous, occasionally thick and tuberous, sometimes from a rhizome or a fleshy or woody caudex. Leaves glabrous, often glaucous [or rarely glandular-pubescent], mostly alternate, occasionally opposite or whorled, often imbricate and sometimes subrosulate, sessile or short-petiolate, often spurred at base, the blades flattened to cylindrical, ovoid, or subglobose, when flattened, linear to lanceolate, oblanceolate, ovate, or suborbicular in outline with entire to dentate margins [rarely spine-tipped]; leaves of vegetative and flowering shoots often dissimilar. Flowers perfect or imperfect (and the plants then dioecious or polygamodioecious), arranged in axillary or terminal, often bracteate, diffuse to compact corymbose, helicoid or scorpioid cymes (often with several helicoid or scorpioid cymes terminating a single flowering stem), in simple or compound dichasia [or rarely solitary or in spikes]; insertion of the floral parts hypogynous. Sepals 4 or 5 [or rarely up to 9], imbricate or valvate in bud, free or connate basally, often fleshy and bractlike or leaflike. Petals 4 or 5 [or as many as the sepals, or sometimes absent in carpellate flowers of dioecious species], free or slightly united basally, erect or patent, yellow, greenish, white, pinkish, purplish [or very rarely blue], usually narrowly elliptic or subulate in outline, sometimes keeled. Stamens 8 or 10 [or twice the number of sepals] in 1 or 2 whorls, free [or those opposite the petals occasionally epipetalous]; filaments subulate to filiform, tapering to the yellowish or reddish anthers. Gynoecium of 4 or 5 [or as many as the number of sepals] erect or divergent carpels, the carpels free [or only slightly coherent basally], tapering into short, slender styles above; ovaries unilocular, with numerous [or rarely 1 or few] ovules on 2-lobed parietal placentae along the adaxial sutures. Fruits erect or divergent follicles, often with stylar beaks, with many [or rarely 1 or few] seeds, dehiscent along the adaxial sutures; seeds usually small, sometimes winged, with fleshy endosperm surrounding the straight embryo; megagametophyte of the Polygonum or Allium type. Base chromosome numbers 4, 5, 6, 7, 8, 9, 10, 11. (Including *Anacampseros* Haw., *Hylotelephium* H. Ohba, *Rhodiola* L., *Tetrorum* Rose.) LECTOTYPE SPECIES: *S. acre* L.; see Hitchcock, Prop. Brit. Bot. 156. 1929. (Name from Latin, *sedere*, to sit or hold fast, in reference to the manner in which numerous species grow on rock outcrops and on walls; said by some to be derived from Latin for to assuage or soothe, apparently in reference to their reputed healing qualities.) — STONECROP, LIVE-FOREVER, ORPINE.

A large genus of some 300 to 600 species (Willis, 1966) widely distributed in the Temperate Zone of the Northern Hemisphere, extending into the Arctic (ca. four species), and into the Southern Hemisphere of the Old World in the equatorial mountains of East Africa and in Madagascar. In the Western Hemisphere species of the genus range into South America in the Andes of Bolivia and Peru. Great concentrations of species are found in western North America; in Mexico, where twenty-eight species are endemic to the trans-Mexican volcanic belt alone (Clausen, 1959); in Europe and the Mediterranean region; and in eastern Asia. In the southeastern United States seven or eight species are native, while three or four additional taxa have been reported as escapes from cultivation. Clausen (1975) recognized twenty-two additional species as native to North America north of the Mexican Plateau, and he also recorded thirteen (both native North American and exotic) taxa as naturalized, while he included fifty-three species in his annotated list of cultivated species.

Largely in response to interest in the species as garden plants, the first modern treatment of *Sedum* was prepared by Praeger (1921), who, in accounting primarily for taxa known in cultivation, laid the basic taxonomic framework for the genus. Praeger distributed the species among ten sections and numerous groups, while Berger (1930), treating the entire genus, recognized twenty-two sections, as well as subordinate series and groups. Fröderström (1930, 1931, 1932, 1935), who prepared the most exhaustive world-wide treatment, recognized two sections (RHODIOLA and TELEPHIUM) but treated the remaining species on a geographic basis, dividing taxa within each major geographic area into two classes (on the basis of erect versus divergent carpels) and numerous subordinate groups. In Praeger's and Berger's classifications, which are generally more utilitarian, are currently in wider use, and also coincide at the sectional rank for our species, the native and adventive southeastern species belong to four sections. In treating the North American species, Clausen (1975) has recognized three of these four subgeneric taxa but has elevated each of them to the rank of subgenus while including the species of the fourth, sect. EPETEIUM Boiss., in subg. SEDUM. He recognizes five sections within subg. SEDUM and two within subg. RHODIOLA.[2]

Section RHODIOLA (L.) Scopoli (*Rhodiola* L., pro gen., *Sedum* subg. *Rhodiola* (L.) H. Ohba) (perennials with deeply rooted, fleshy or woody caudices terminated by clasping, well-developed or reduced, scalelike leaves with annual, leafy flowering stems developed in their axils, the mature follicles erect, with stout stylar beaks) is primarily a Eurasian group that is represented in North America by only two (or perhaps three) species. *Sedum Rosea* (L.) Scopoli (*Rhodiola Rosea* L., *Sedum Rhodiola* DC., *S. roanensis* Britton, *S. Rosea* var. *roanensis* (Britton) Berger, *Rhodiola roanensis* (Britton) Britton), $2n = 18, 22, 32, 33, 36$, is a wide-ranging circumpolar species, with a discontinous distribution at higher altitudes in mountainous regions, that occurs throughout much of Asia, northern Europe, and arctic and boreal North America. In our area, it has been recorded from over 6,000 feet on Grandfather Mountain, North Carolina, and on Roan Mountain, on the North Carolina-Tennessee boundary. These southern localities, where *S. Rosea* grows in moist soil in crevices and on rock ledges, usually on north-facing cliffs, are some 500 miles south of the nearest known populations in Bucks County, Pennsylvania. Farther north it occurs at high elevations in New York, Vermont, and northward along the coast of Maine into Canada. In western North America, *S. Rosea* extends southward in the Cordillera into California, Colorado, and New Mexico, and in the Rocky Mountains (where it is sometimes segregated as *S. integrifolium* (Raf.) A. Nelson (*Rhodiola integrifolia* Raf., *S. Rhodiola* Torrey, not DC.) or treated as *S. Rosea* subsp. *integrifolium* (Raf.) Hultén), it is often sympatric with *S. rhodanthum* A. Gray (*Clementsia rhodantha* (A. Gray) Rose), $2n = 14$, the second representative of the section in North America.

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[2] Although Clausen (1975, p. 474) proposed *Sedum* subg. RHODIOLA, the change in status had been proposed by H. Ohba (1975, p. 285) some months before the publication of Clausen's treatment. Despite this, Ohba (1977) credits the combination to Clausen.

Characterized by usually imperfect, four-merous flowers in dense, terminal corymbose cymes and by fleshy or woody caudices that reputedly emit an odor of roses when dried, plants of *Sedum Rosea* are dioecious or occasionally polygamodioecious; individuals and entire populations with perfect flowers occur in some areas. The petals are greenish or yellowish, often tinged red at the apex, or deep red, and the numerous, closely spaced, glaucous, alternate leaves of the erect stems are oblanceolate, with acute apices and entire or irregularly dentate margins.

Extremely polymorphic over its wide geographic range, *Sedum Rosea* consists of numerous races that differ from one another primarily in flower color, leaf-margin dentation, and plant size and habit. Numerous segregate taxa have been proposed, particularly from Asia. Britton & Rose (1903, 1905) considered the southern Appalachian populations to comprise a distinct species (*S. roanensis*, as a species of *Rhodiola*); they also recognized four segregate species in western North America. Hultén (1945), however, contended that the majority of segregate taxa should be considered informally as local races, while others should, at most, be treated at the subspecific or varietal rank.

Sedum Rosea is also variable cytologically, and Uhl (1952) has shown that two chromosome races, one with $2n = 22$, the other with $2n = 36$, are widespread in North America. Wiens & Halleck (1962), however, have reported that Rocky Mountain plants of *S. Rosea* have $2n = 32$, and a count of $2n = 18$ has been reported by Sokolovskaya & Strelkova (1960). Other than inconsistent differences in flower color, plant sexuality, and habit, the cytological differences appear to lack morphological correlations, yet the 22-chromosome race occurs in glaciated northeastern North America (and in Eurasia), while the 36-chromosome race is apparently confined to unglaciated areas of the continent. Plants from our area remain uninvestigated cytologically, and, although it has been questioned whether these southern populations are still extant (Wherry, 1934; Uhl, 1952), Clausen (1975) reported seeing two plants on Roan Mountain in 1972.

Section Telephium S. F. Gray (*Sedum* subg. *Telephium* (S. F. Gray) R. T. Clausen, *Hylotelephium* H. Ohba) (perennials from caudices lacking scalelike leaves, with slender to thick fusiform roots, producing erect, rarely decumbent, usually annual, leafy flowering stems; flowers perfect, 5-merous, with erect, stipitate carpels, the mature follicles erect, with slender stylar beaks) is also widely distributed in temperate regions of Eurasia and is represented in our flora by *Sedum telephioides* Michaux (*Anacampseros telephioides* (Michaux) Haw., *Hylotelephium telephioides* (Michaux) H. Ohba), $2n = 24$. The only species of the section indigenous to North America, *S. telephioides* grows on rock ledges and in crevices on exposed and shaded cliffs, and on stony slopes in rich woods in the mountains and adjacent upper Piedmont from southern Pennsylvania southward into Georgia; it is also known from limestone bluffs along the Ohio River in southern Indiana (Harrison County) and from southern Illinois.[3]

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[3] House (Annot. List Pl. N. Y. 376. 1924) pointed out that records for *S. tele-*

Blooming in late summer and fall, *Sedum telephioides* is rather variable vegetatively but is easily recognized among our native sedums by its erect stems with flattened, mostly alternate or sometimes opposite, occasionally glaucous, broadly ovate leaves with subentire to coarsely toothed margins, and its numerous flowers arranged in corymbiform cymose inflorescences 2.5–8(–14) cm. broad. The carpels are pinkish, subtended by nectariferous scales about as broad as long, and the sepals and stamens are shorter than the pink to whitish petals.

Closely allied to *Sedum Telephium* L., a wide-ranging Eurasian species, and the numerous (up to 25) additional Eurasian taxa included within this complex (several of which have been variously either segregated from or included within *S. Telephium*), S. *telephioides* has been retained as a distinct species by American botanists despite the suggestions of both Praeger and Berger that it is probably only a variety of *S. Telephium*. Like the *S. Rosea* group, the *S. Telephium* complex is exceedingly variable both morphologically and cytologically, and its classification and nomenclature are both confusing and in need of careful study. As a group, the Eurasian taxa can reputedly be distinguished from *S. telephioides* by their fusiform roots, their flowers with the sepals scarcely one-third as long as the petals, their stamens about equaling or exceeding the petals, and their nectariferous scales longer than broad.

Of the taxa included within the *Sedum Telephium* group, *S. telephioides* appears to be most closely allied to *S. Telephium* subsp. *alboroseum* (Baker) Fröd. (*S. erythrostictum* Miquel, *S. alboroseum* Baker, including *S. spectabile* Boreau, *fide* Fröderström, *Hylotelephium erythrostictum* (Miq.) H. Ohba), $2n = 48, 50, 51$, of China, Manchuria, and Japan, which has been reported as an escape from gardens in northeastern North America, southward into Virginia and North Carolina. An herbaceous perennial with spreading to procumbent stems to 60 cm. tall, with alternate, opposite, or whorled leaves and pinkish white flowers in flat corymbose cymes, subsp. *alboroseum* flowers in late summer and fall and is also closely linked to *S. Telephium* subsp. *Telephium* var. *purpureum* L. (*S. Telephium* subsp. *purpurascens* (Koch) Areschoug, *S. purpureum* (L.) Schultes, *S. purpurascens* W. D. J. Koch), $2n = 36, 48$.[4] Also a common garden plant, *S. Telephium* var. *purpureum* has been reported as an escape and persisting outside of cultivation near waste heaps in Warren County, North Carolina. Native to Europe, plants of *S. Telephium* var. *purpureum* are stout, glabrous herbs from fusiform roots, with alternate, broadly oblong or elliptic leaves with coarsely and irregularly toothed margins and flowers with purplish red to rosy petals in dense, terminal and lateral, subglobose cymes. Unlike those of *S. telephioides*, the leaves of *S. Telephium* var.

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phioides from western and central New York state are generally attributable to *S. Rosea*. One substantiated report from Dutchess County is probably based on a plant escaped from cultivation (cf. Wherry, 1936).

[4] Material determined to be $2n = 48$ tentatively assigned to subsp. *Telephium* var. *purpureum* (as subsp. *purpurascens* (Koch) Areschoug) by Jalas & Rönkkö (1960).

purpureum are reduced in size up the flowering stems. *Sedum Telephium* has also been listed as persisting outside of cultivation in Knox and Sevier counties, Tennessee, but it is not known to which subspecies these plants should be assigned. Allard (1932, 1940), moreover, contended that true *S. Telephium* is a long-day plant that rarely blooms in gardens south of New England. It is obvious that the reports of taxa of this complex in our area should be examined critically during the course of an overall study of the group.

The majority of species of *Sedum* have been placed in sect. SEDUM (*Seda Genuina* W. D. J. Koch, sect. *Eusedum* Boiss., subg. *Sedum* fide R. T. Clausen) (annual or usually perennial herbs or subshrubs with creeping rhizomes, cespitose sterile stems, and erect or ascending flowering stems; flowers perfect, the mature follicles divergent). This section is represented in the southeastern states by four native species and two adventives that have become naturalized.

Sedum pulchellum Michaux (including *S. vigilmontis* Small), $2n = 22$, 44, 66, occurs primarily on limestone, but also grows on granitic and siliceous outcrops in open and wooded habitats from western Virginia through Kentucky and Tennessee to southern Illinois, Missouri, and Kansas, and southward into northwestern Georgia, northern Alabama, Arkansas, Oklahoma, and Texas. *Sedum pulchellum* is usually a winter annual or occasionally a biennial or perennial due to persistence of vegetative shoots. Its seeds germinate in the fall and produce small, lax rosettes of flat, greenish gray, oblong-spatulate leaves (FIGURE 1, a). Early in spring, decidedly different erect flowering stems develop with narrowly linear, cylindrical, terete leaves with auriculate or sagittate bases (FIGURE 1, b). These leafy stems, 10–30 cm. high, are terminated by three (rarely to seven) widely divergent, recurved, secund scorpioid cymes 3–4 cm. long comprising many four-merous flowers with whitish to deep pink or purplish petals that are about twice as long as the small sepals.

In their vegetative, over-wintering stage, plants of *Sedum pulchellum* have been confused with *S. Nevii* A. Gray (*S. Beyrichianum* Masters (?), *S. Nevii* var. *Beyrichianum* (Masters) Praeger (?)), $2n = 12$, a narrow endemic known with certainty from only five localities (three in Alabama, one in southeastern Tennessee, and one in extreme west-central Georgia near the Alabama line). A slender, only slightly glaucous perennial with loose, sterile rosettes of leaves 1–5 mm. wide, flowering stems with 12–40 narrowly oblanceolate or linear-oblanceolate, usually subterete leaves 3–19 mm. long, 1–3 mm. wide, white, four-merous flowers in two or three slender helicoid cymes terminating flowering stems, and seeds 0.5–0.6 mm. long, *S. Nevii* grows on exposed and/or shaded cliffs and rock ledges. Until Baldwin's (1942) cytological investigations revealed that the Alabama plants are diploids with $2n = 12$, it was generally assumed that *S. Nevii* had a wider range in the eastern United States. Virginia plants referred to *S. Nevii*, however, proved to be diploids with $2n = 28$, and, as a result of this chromosomal difference and very subtle morphological dissimilarities, Clausen (1946) segregated the Virginia populations as *S. glaucophyllum*.

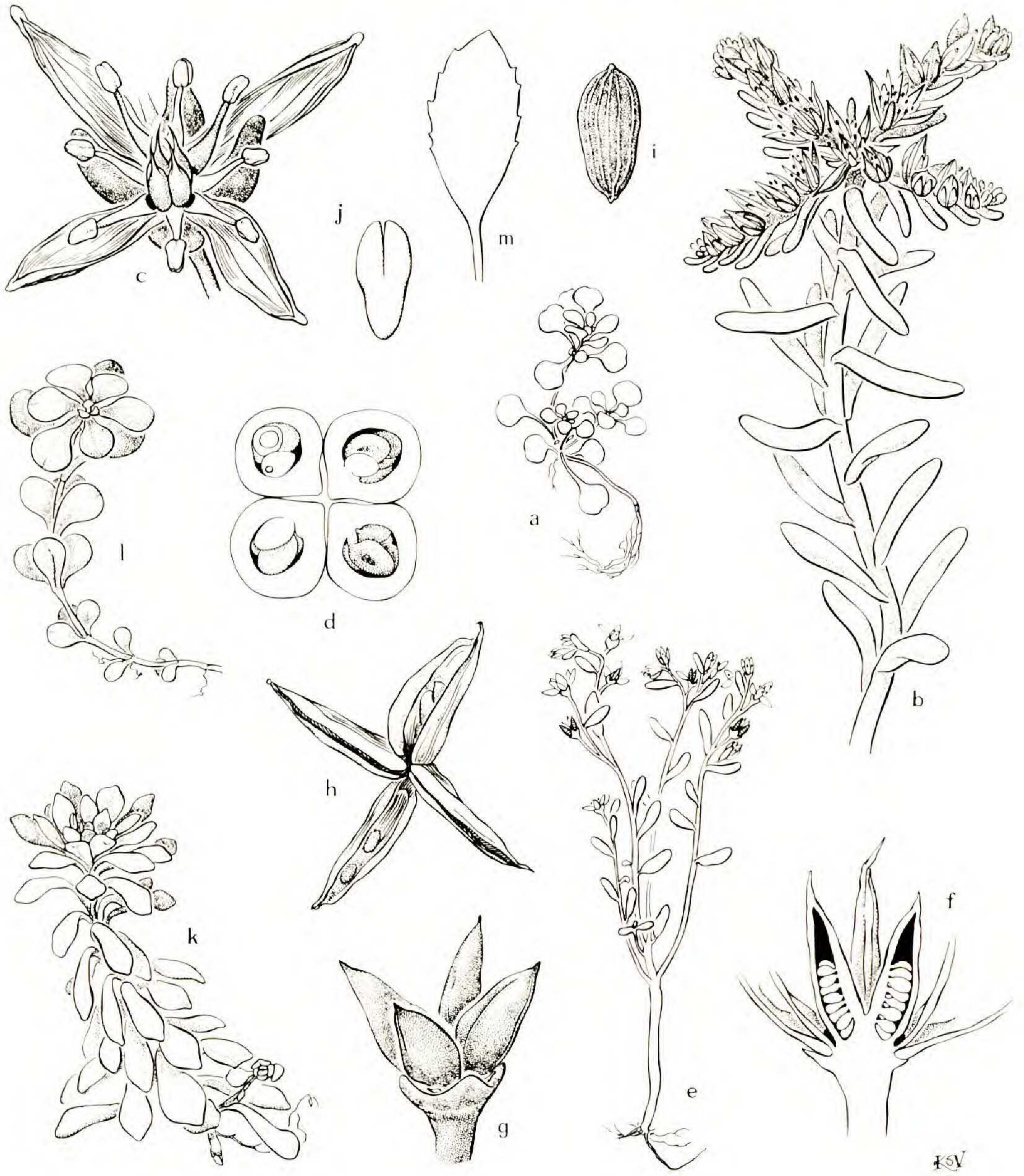

FIGURE 1. **Sedum**. a–d, *S. pulchellum*: a, over-wintering rosette, × ½; b, flowering shoot, × 1; c, flower, × 5; d, cross section through four carpels of gynoecium, × 20. e–j, *S. pusillum*: e, habit of mature plant, × 1; f, longitudinal section through immature follicles (note nectaries, solid black, at base of carpels), × 6; g, immature follicles, × 6; h, mature, dehisced follicles, × 6; i, seed, × 25; j, embryo, × 25. k, *S. glaucophyllum*, leafy shoot, × 1. l, *S. ternatum*, leafy shoot, × ½. m, *S. telephioides*, outline of leaf, × ½.

Moreover, western records for *S. Nevii* in southern Illinois and Missouri have resulted from confusion with *S. pulchellum* (cf. Wherry, 1934, 1936).

Further cytological investigations by Uhl (1970) have revealed chromosome numbers of $2n = 28$, 44, and 56 within *Sedum glaucophyllum*, which is now known to range from southern Maryland, southward through the mountains and adjacent Piedmont of West Virginia, Virginia, and North Carolina, where it is known from Rockingham and Surrey counties. A glaucous perennial with dense, sterile rosettes of leaves 2–7 mm. wide, flowering stems with 30–50 flat, oblanceolate leaves 5–25 mm. long and 2–6 mm. wide, white, four-merous flowers in three or sometimes four slender helicoid cymes terminating the flowering stems, and seeds 0.5–0.9 mm. long, *S. glaucophyllum* grows in moist rock crevices on both sunny and shaded cliffs.

Acceptance of the distinct species status of *Sedum glaucophyllum* has been tentative since morphologically it is practically indistinguishable from *S. Nevii*, and the characters used to separate it are largely qualitative. Clausen himself (1946) cautioned that ". . . if the morphological and cytological differences are not correlated . . . the classification again must be revised and *S. glaucophyllum*, though a genetical species, would need to be handled taxonomically as a synonym under *S. Nevii*, since it would not be a practical unit capable of recognition by ordinary observation." However, since *S. Nevii* sensu stricto is a narrowly restricted endemic, the use of the name *S. glaucophyllum* for plants throughout the distinct, more northeastern range of that taxon is facilitated on a geographic basis and seems justified considering the state of our biological knowledge of both taxa.

Another species of sect. SEDUM, *Sedum ternatum* Michaux (*Anacampseros ternata* (Michaux) Haw.), $2n = 16, 24, 32, 48$, is widely distributed throughout the eastern United States, from New Jersey and Pennsylvania, west through Ohio and Illinois to Missouri, and southward to the Carolinas, Georgia, and Arkansas. Easily recognized by its flat, elliptic to spatulate or rounded leaves usually in whorls of three on sterile shoots, and its obovate to spatulate leaves on the erect flowering stems, *S. ternatum* is a procumbent, mat-forming perennial with white, four-merous flowers with crimson or purplish anthers. The flowers are usually arranged in three terminal scorpioid cymes. The plant often occupies rich, moist sites in woodlands and frequently grows on rocky slopes and along stream banks where it sometimes forms extensive, carpet-like stands. Baldwin (1942) discovered the existence of four chromosome races: diploids ($2n = 16$), triploids ($2n = 24$), tetraploids ($2n = 32$), and hexaploids ($2n = 48$). While these races lack morphological correlations, the diploid race (West Virginia, Kentucky, and Virginia) and the hexaploid (one locality near Tuscaloosa, Alabama) have limited geographic ranges in contrast to the widespread tetraploid and the sporadic occurrence of triploid plants.

Sedum sarmentosum Bunge, a native of northern China and Japan, is also a prostrate, mat-forming perennial with long, creeping sterile shoots with leaves in whorls of three and erect flowering stems. Its flowers, however, are arranged in terminal compound cymes and are bright yellow. Occasionally cultivated as an ornamental, *S. sarmentosum* has been reported as naturalized in a few dry, open, rocky areas in the mountains of North Carolina. Small (1933, p. 588) probably confused this species with *S. mexicanum* Britton (*S. sarmentosum* Masters, not Bunge) when he said that it (*S. mexicanum*) ". . . is often cultivated and occasionally escapes from gardens" in the Southeastern States.

Another adventive, *Sedum acre* L., $2n = 16, 40, 48, 60, 80, 100, 120$, is native to a wide area of the Old World in Europe, northern Asia and Asia Minor, and northern Africa. Plants of this species are small, creeping, mat-forming, evergreen perennials, with bright yellow flowers produced in two or three terminal cymes. They can be recognized by the overlapping, alternate, flattish, deltoid leaves that are broad and slightly spurred at the base. One of the most widely cultivated sedums in rockeries and on walls, *S. acre* has apparently become naturalized in Avery and Mitchell counties, North Carolina.

Section EPETEIUM Boiss. (sect. *Procrassula* (Griseb.) Schönl., *pro parte*; *Procrassula* Griseb.) (annual or biennial herbs with slender, poorly developed root systems, the flowering plants lacking sterile shoots, with alternate, flattened or cylindrical leaves and branched cymose, corymbiform, or dichasial inflorescences comprising several to numerous 4–9-, mostly 5-merous flowers with white, yellow, red, or blue petals) is sometimes included within sect. SEDUM and is represented in our area by two species. *Sedum pusillum* Michaux (*Tetrorum pusillum* (Michaux) Rose), $2n = 8$, is a diminutive winter annual endemic to the Piedmont of the Carolinas and Georgia. In this region *S. pusillum* is totally restricted to granitic flat-rock communities, and it is sometimes confused with *Diamorpha Smallii* Britton (q.v.). *Sedum pusillum* is typically found growing in the partial shade of pines or *Juniperus virginiana* L. at the margins of the rock outcrops and in sheltered depression pits on outcrop surfaces, often near vernal pools. *Diamorpha Smallii*, on the other hand, grows in exposed depression pits with very shallow soils. A small, early-spring-flowering, usually branched herb 4–12 cm. high with bluish green (or sometimes reddish) cylindrical leaves and four- or rarely five-merous white or pinkish flowers with red anthers arranged in small helicoid cymes or simple or compound dichasia, *S. pusillum* differs in several significant anatomical and morphological features from *Diamorpha*. These differences, several of which are diagnostic in the field, are discussed under *Diamorpha*. The diploid chromosome complement of $2n = 8$ known for *S. pusillum* is the lowest diploid number recorded in the Crassulaceae (Baldwin, 1940).

Sedum Nuttallianum Raf. (*S. Torreyi* G. Don, *S. sparsiflorum* Nutt. in Torrey & Gray), $2n = 20$, also a diminutive winter annual, ranges from Arkansas and Missouri, southward into Oklahoma and Texas. Flowering from April to July, *S. Nuttallianum* grows in the shallow soils of chert and sandstone glades and ledges and in the clayey soils of pasturelands. Individuals of *S. Nuttallianum* are small plants 5–15 cm. high, usually branched from the base, with short, pale, silvery green, cylindrical, alternate leaves and sessile or short-pedicellate, five-merous flowers with lanceolate yellow petals arranged in two to five terminal cymes. Although the individuals are small, the plants commonly grow in large, dense populations and give an overall effect in the field of a low, mat-forming perennial.

Despite continued investigations of the genus, *Sedum* remains extremely complex taxonomically and confusing nomenclaturally. While the subgeneric classification is not without problems, particularly some concerning the limits and validity or potential generic status of certain sections, the greatest confusion appears to center around the definition of species and subspecific taxa. Certainly some of the confusion is the result of the fact that "dried specimens can be the source of erroneous impressions concerning the dimensions and shapes of structures, as well as the habits of plants . . ." (Clausen, 1959, p. 337). In addition, many species are narrow endemics, while others are extremely wide-ranging and exhibit a polymorphism that appears to be proportional to the extent of the geographic range. Furthermore, individuals of a given taxon may appear quite different from one another depending upon their habitats and the time of year the plants are observed or collected. The color of the stems and foliage, for example, is prone to change, usually becoming reddish under dry conditions, with age, or when grown in intense light.

But, as pointed out by Uhl (1961), "the most conspicuous problem is the frequency with which heteroploidy occurs within what many authors have regarded as a single species. . . ." While this phenomenon is characteristic of the Crassulaceae in general, it is particularly evident in *Sedum*, where both polyploidy and aneuploidy have been documented for numerous species, several of which are native to our area. Furthermore, every gametic chromosome number from $n = 4$ to $n = 38$ is known in the genus. However, *S. spathulifolium* W. J. Hooker, $2n = 30$, is cited as an exception to the rule, inasmuch as it is a wide-ranging species (Vancouver Island, south to southern California) that apparently has the same chromosome number over its entire area (Uhl, 1961b).

As a possible explanation of the usual lack of morphological correlation with the heteroploid cytological condition found in numerous species, Uhl (1961b) suggests that these taxa are presently undergoing rapid evolution and that "each karyotype has not yet evolved its own distinctive genotype and phenotype. . . ." This hypothesis gains support from the fact that the usual habitats of species of *Sedum* are cliffs and rock outcrops, habitats that are discontinuous and unstable in terms of geologic time and, as a result, are probably conducive to rapid evolutionary rates. Likewise, Clausen (1959) suggests that the morphological and physiological differences between the closely related species endemic to the trans-Mexican volcanic belt are largely due to gene mutations, while changes involving chromosome number have led primarily to genetic isolation between sympatric taxa. Investigations employing electrophoretic techniques might give support to these interpretations.

While the chromosomes of *Sedum* are generally small, Uhl (1961) and Uhl & Moran (1972) point out that they seem to possess localized kinetochores, ruling out the possibility that the heteroploid condition is the result of diffuse kinetochores and chromosome breakage like that documented for *Carex* (Cyperaceae) (Davies, 1956). Levan (1933) reported heteromorphic sex chromosomes for a single plant of *S. Rosea* from a dioecious population, but in his 1952 report, Uhl could not distinguish specific sex chromosomes.

In their cytological survey of Japanese and South Korean Crassulaceae, Uhl & Moran (1972) calculated the approximate nuclear volume of cells of taxa within two complexes of *Sedum*. A nearly proportional increase of nuclear volume was found in sect. AIZOON, a complex comprising diploids (where $n = 16$) to apparent heptaploids, suggesting that the change in chromosome number within this group is the result of "multiplication of the more or less complete genome." This situation is in contrast to that encountered in *S. polytrichoides* Hemsley ex Hemsley & Forbes, *sensu lato*, where no clear relationship between chromosome number and nuclear volume was evident. Uhl & Moran speculate that in this highly dysploid species, where plants are known to vary from $n = 11$ to $n = 35$, "very extensive rearrangement and repackaging of essentially the same amount and kind of chromosomal material, probably chiefly by translocations, have accompanied and made possible the many changes in chromosome number in this complex."

Interspecific hybridization, except within sect. TELEPHIUM, is thought not to occur in nature, and there have been no attempts to produce artificial hybrids utilizing cultivated materials (Evans, 1971). Even within taxa exhibiting polyploidy it has generally been concluded that the polyploid condition has been achieved through autopolyploidy and not through allopolyploidy. Certain hypotheses concerning the origins of some taxa, however, have been advanced that are based on the assumption that interspecific hybridization has occurred. Notable among these hypotheses is Baldwin's (1940) suggestion that *Diamorpha Smallii*, $2n = 18$, is the amphidiploid product of "fusions between the 4- and 5-chromosome tendencies" within *Sedum* as represented by *S. pusillum* and *S. Nuttallianum*, respectively.

The scant data concerning floral biology of *Sedum* indicate that there is a range from proterogyny and homogamy to marked proterandry. In proterandrous flowers the anthers of the outer whorl of stamens dehisce first, followed by the slightly delayed dehiscence of the anthers of the inner whorl. The movement of the stamens to an erect position over the carpels just before dehiscence and their subsequent return to the periphery of the flower afterward are suggestive of similar movements observed in flowers of several genera of subfam. Saxifragoideae of the Saxifragaceae. Although the maturation and receptiveness of the stigmas and the dehiscence of the anthers are usually not synchronous, self-pollination may occasionally occur; however, no studies have been located that deal with compatibility systems within the genus.

Nectar is secreted by the small, scalelike glands that subtend the carpels (the glands considered to be dorsal outgrowths of the carpels), and the few recorded observations suggest that visitors attracted to the flowers are usually dipterans, hymenopterans, and lepidopterans.

Dispersal of seeds from the mature, dehisced follicles is probably by wind action that sets up short-term vibrations of the follicles. The seeds are small, and those of *Sedum Rosea* are narrowly winged at each end. The low, often creeping, vegetative shoots of numerous species root at the nodes, and propagation and dispersal undoubtedly occur frequently by vegetative means. Both pieces of stem and individual detached leaves of most species develop adventitious roots and shoots, and Yarbrough (1936) found that in leaves the mode of origin of these structures is through the activity of a secondary meristem that develops from vacuolated, differentiated parenchyma. This "regeneration" is in contrast to the formation of the plantlets produced along the leaf margins or at leaf or petiole bases in species of *Kalanchoë*, which are the result of the activity of a residual primary meristem.

The vascular anatomy of the flowers of a relatively large number of species was investigated by Quimby (1971), who placed these taxa in four groups based on the number of whorls of traces supplying the flowers. The majority of species (37) have four whorls of traces (Group III), while others have six (Group I, the presumed underived condition found in species of sect. TELEPHIUM), five (Group II), or three (Group IV) whorls. Vertical compression of the receptacle has apparently led to the reduction in the number of whorls. Additional study of the vascularization of flowers of *Sedum pusillum* (Sherwin & Wilbur, 1971), conducted to help clarify the generic lines between *Sedum* and *Diamorpha*, showed that *S. pusillum* does not fit into either Group III or Group IV. Sherwin & Wilbur suggest that the vascular pattern found in flowers of *S. pusillum*, which Quimby placed in Group III, is perhaps derived from the basic Group III pattern. Furthermore, their work indicates that more detailed investigations of individual species may show that floral vascularization in *Sedum* is more complex and variable than outlined by Quimby.

The carpels of *Sedum*, each of which is supplied by five vascular bundles, have been considered primitive since they are open during ontogeny, closing only during later development when the margins along the adaxial sutures are only slightly fused, and the marginal epidermal layers remain distinct (Eames, 1931). Henslow (1891) reported that the ventral carpel traces in *Sedum Telephium* are not inverted (a condition encountered in *Silene* and *Dianthus* [Caryophyllaceae] and in some species of *Rhododendron* subg. *Anthodendron* [Ericaceae]), but Subramanyam (1955) detected only inverted traces in species he examined. Relatively few investigations of the general vegetative anatomy of *Sedum* have been undertaken; see the works of Solereder (1899) and Metcalfe & Chalk (1950) for some details and references to most studies, as well as the more recent papers by Piaget (1966) and Jensen (1968).

Aspects of megasporogenesis and embryology of *Sedum* coincide with the general pattern given for the family with only a few significant exceptions. In *S. Telephium* subsp. *fabaria* (W. J. D. Koch) Kirschleger and *S. populifolia* Pallas (*Hylotelephium populifolium* (Pallas) H. Ohba), a subshrub from eastern Asia, an Allium-type megagametophyte has been reported to develop from the chalazal dyad cell, while in other investigated species a monosporic Polygonum-type is produced. Endosperm formation is *ab initio* Cellular and a chalazal haustorium is developed, but Subramanyam (1963) found that in *S. ternatum* the haustorium remains 1-nucleate. *Sedum ternatum* is also distinguished by the presence of apical "caps" on the hooked synergids, structures that have been reported elsewhere only for *Helianthemum vulgare* (Cistaceae) and species of *Ribes* (Saxifragaceae or Grossulariaceae). See Subramanyam's articles (1955, 1963) for additional details and information about microsporogenesis.

Pollen of some European species of *Sedum* has recently been examined by 't Hart (1974), who found the grains to be 3- or rarely 2- or 4-zonocolporate. The sexine a, a tectum, is ornamented with short striae in a rugulate pattern, and, although considerable variation in morphology was evident, 't Hart concluded that the range of variation encountered within a single taxon, and occasionally within a single sample, equaled that found during the survey. All of the species examined (including one miscellaneous American species) belong to one variable pollen type and form a continuous morphological series that can only arbitrarily be divided into subtypes. However, 't Hart ventures to assert that within the *Rupestria* series species with low base chromosome numbers have relatively underived pollen subtypes, while those species with higher base numbers exhibit derived pollen subtypes. This correlation was not evident in the *Sedum acre* group, suggesting less phylogenetic unity within that taxon.

Determination of the generic relationships of *Sedum* is dependent, in large measure, on the delimitation of the genus and the several groups that have variously been either segregated from or included within the genus. At one extreme, as Moran (1942) points out, Kuntze (1898) concluded ". . . that all the species of the Crassulaceae with free carpels, i.e., practically the entire family, were best placed in the one genus *Sedum*." Conversely, there has been a continued tendency on the part of authors of floristic works (culminating in the treatments of Britton & Rose, 1903, 1905) to accord generic status to small groups or single species that within a local area appear distinct. In other instances, species or groups of species once included within *Sedum* have been removed and merged with other genera as warranted by careful analyses of relationships (e.g., *Hasseanthus* Rose, a segregate of *Sedum*, is now treated as a subgenus of *Dudleya* Britton & Rose, a member of subfam. Echeverioideae Berger).

In particular, sect. RHODIOLA is often recognized as a distinct genus, especially when the species of that section with which floristic workers are concerned have four-merous, imperfect flowers. *Sedum rhodanthum* of the Rocky Mountains (its flowers five-merous and perfect), like several of the Asiatic species, clearly belongs to the section as emended by Praeger, and it is transitional to species in other sections of the genus. However, despite the obvious similarities, *S. rhodanthum* was removed to the monotypic genus *Clementsia* by Rose (in Britton & Rose, 1903) in an attempt to create greater unity within sect. RHODIOLA, which Britton and Rose also treated as a genus. Similarly, species of sect. TELEPHIUM, some of which are transitional to sect. SEDUM, have been transferred to the segregate genus *Telephium* Hill, not L., or to *Anacampseros* P. Miller, and Ohba has recently placed these species in the new genus *Hylotelephium.* In our area, in addition to recognizing *Diamorpha*, Britton and Rose also segregated *S. pusillum*, placing it in the monotypic genus *Tetrorum* Rose because of its annual duration and its four-merous flowers.

Certainly some of the problems of delimiting acceptable genera are due to the fact that affinities within the entire family appear to be interlinear as well as linear (Baldwin, 1939). Nonetheless, it is apparent that in the New World the closest affinities of *Sedum* are largely with genera of subfams. Sedoideae and Echeverioideae. Most of the closely allied genera of the Sedoideae share the characteristic terminal flowering stems and flowers with free, spreading petals, while genera of subfam. Echeverioideae are usually characterized by lateral flowering stems and by flowers with basally connate, erect or spreading petals. *Sedastrum* Rose (*Sedum* sect. *Sedastrum* (Rose) Berger) is distinguished from *Sedum* by its persistent, rosulate basal leaves and its flowers with enlarged nectaries and white petals, while *Parvisedum* R. T. Clausen (*Sedella* Britton & Rose, not Fourreau; *Sedum* sect. *Sedella* (Britton & Rose) Berger), a small genus of four annual species of the California mountains, is characterized by its carpels with solitary ovules. *Diamorpha* differs from *Sedum* in several significant respects discussed elsewhere, but the contrasts between *Villadia* Rose (including *Altamiranoa* Rose) are less concrete. Consisting of about 45 species of Mexico, Central America, and the Andes of South America, species of *Villadia* produce terminal inflorescences, and in the last analysis the genus is separated from *Sedum* only on the basis of the degree of basal connation of the petals (Moran, 1971). *Lenophyllum* Rose, a small genus of about five species restricted to the Gulf Coastal Plain of southern Texas and Mexico, is characterized by opposite leaves and flowers arranged in terminal racemose or spicate cymes. In habit the species of *Lenophyllum* resemble species of *Echeveria* DC. (ca. 143 species ranging from Texas to the Andes of South America), but Uhl & Moran (1953) suggest that *Lenophyllum*, which was once placed in subfam. Echeverioideae, is best removed to subfam. Sedoideae. Clausen (1975) contends that the genus was probably derived from the same phyletic line that gave rise to *Villadia, Echeveria*, and *Pachyphytum.*

While the relationships of the several genera of subfam. Echeverioideae are taxonomically complex and cytologically diverse and complicated (Uhl & Moran, 1953), it would appear that *Echeveria* is closely allied to *Sedum.* Walther (1936, 1972) speculates that *Echeveria* was derived from species not unlike certain subshrubby species of *Sedum* belonging to sects. PACHYSEDUM Berger and DENDROSEDUM Berger, which are endemic to Mexico (the center of diversity of *Echeveria*) and share the characteristic lateral flowering stems of subfam. Echeverioideae.[5] Although hybrids between species of *Echeveria* and *Sedum* sects. PACHYSEDUM and

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[5] Walther employs the name *Sedum* sect. *Bergerosedum* Walther to refer to those species of the two sections mentioned above; some of these species were also treated by Rose as comprising the segregate genera *Cremnophila* and *Corynephyllum.* The sectional name, however, was nomenclaturally superfluous when published. In ad-

DENDROSEDUM have been produced (Walther, 1953; Uhl, 1966, 1967, 1970; one placed in the hybrid genus × *Sedeveria* Walther), this evidence of close relationship loses some of its potential significance due to the numerous intergeneric hybrids produced between *Sedum* and other genera of subfam. Echeverioideae (Uhl, 1966; Uhl & Moran, 1973; Knobloch, 1972).

Uhl & Moran (1973), considering the cytological evidence, indicate that many Mexican species of *Sedum* (where $x = 29–36$) belong to a comparium that includes, in addition to *Echeveria* (where $x = 27–34$), species of *Pachyphytum* Link, Klotzsch, & Otto, $x = 31–33$ (12 species of Mexico distinguished by pairs of scales on the adaxial surfaces of the petals), *Thompsonella* Britton & Rose (*Echeveria* sect. *Thompsonella* (Britton & Rose) Berger) (two species of south-central Mexico with the flowers arranged in a panicle or thyrse and with red lines on the adaxial surfaces of the petals), and *Graptopetalum* Rose (*Byrnesia* Rose; *Sedum* sect. *Graptopetalum* (Rose) Berger; *Echeveria* sect. *Graptopetalum* (Rose) Kearny & Peebles), $x = 30–35$ (11 species of Arizona and Mexico with red dots, often in transverse bands, on the adaxial surfaces of the petals). Uhl & Moran (1973, p. 655) state that the chromosomes of these taxa ". . . apparently have considerable homology for one another, as shown by their ability to pair, often more or less normally, in intergeneric hybrids. Very likely it was from an ancestral plexus with such [base chromosome] numbers, in the more primitive genus *Sedum*, that the other four genera were derived."

Plants of *Sedum Telephium* and other species are occasionally used as greens in salads, and Uphof (1968) reports that the Eskimos of Alaska eat the leaves of *S. Rosea* fresh, soured, or in oil. *Sedum acre* has apparently been used as a laxative, while the juice from plants of the Mexican and Guatemalan *S. dendroideum* Moç. & Sessé is astringent and has been used to harden gums and to treat chilblains and dysentery. The juice of this species has also been reported by Palarea (1954, as *S. praealtum* A. DC.) to cure opacities of the lens and cornea in humans. In addition, various medicinal uses have been reported for *S. Rosea*, and numerous studies of the chemical and physiological effects of this species have been conducted, primarily by Russian investigators; see Clausen (1975) for an extensive list of Russian references.

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2. Diamorpha Nuttall, Gen. N. Am. Pl. 1: 293. 1818.

Diminutive, characteristically red-pigmented winter annuals from slender primary roots and well-developed, fibrous secondary roots; plants developing ill-defined, over-wintering basal rosettes in fall, the erect or ascending, branched or unbranched stems developing in spring. Leaves alternate, sessile, cylindric-ovoid or cylindric-oblong, succulent, with entire margins and rounded apices (often appearing acute when dried). Flowers perfect, on short, distally thickened pedicels, arranged in leafy, compound cymose inflorescences or variously reduced to a simple dichasium or a single terminal flower. Sepals 4, very small, deltoid or deltoid-linear, persistent in fruit. Petals 4, alternate with the sepals, white or pinkish, strongly cucullate, the 4 opposite anthers held in small distal pockets until late in anthesis. Stamens 8, obdiplostemonous; filaments tapering gradually to the basifixed, reddish anthers. Gynoecium of 4 (rarely 5) carpels; carpels united basally for ca. 1/3 their length, free above, each constricted into a short, beaklike style, the styles terminated by small capitate stigmas, apparently shriveling after pollination; ovary superior, 4- (rarely 5-) locular in the syncarpous region, each carpel 1-locular in the apocarpous region; ovules numerous on axile placentae below, pendulous on marginal placentae above. Carpels divergent, becoming obliquely oriented in fruit, producing a 4- (or 5-) beaked follicetum, each follicle dehiscing extrorsely by a tear-shaped, flaplike valve. Seeds several in each follicle, small, pyriform; seed coat reddish brown, finely granulate-striate; embryo large, with rounded cotyledons. Base chromosome number 9. TYPE SPECIES: *D. pusilla* sensu Nutt. non Michaux = *D. Smallii* Britton (cf. Wilbur, 1977). (Name from Greek, *di*, two, and *morphe*, form or shape, possibly in reference to the initial confusion of the type species with *Tillaea* or, more likely, *Sedum pusillum*; Baldwin (1940) interpreted the name as signifying "deformed or contrary formed.") — ELF-ORPINE.

An arresting monotypic genus endemic to the southeastern United States in North and South Carolina, Georgia, Alabama, and southeastern Tennessee. Growing in dense, usually pure populations in the shallow, humus-free soils of depression pits on exposed rock surfaces, *Diamorpha Smallii* Britton (*Tillaea ? cymosa* Nutt., *Diamorpha cymosa* (Nutt.) Britton ex Small, *D. pusilla* (Michaux) Nutt., *Sedum cymosum* (Nutt.) Fröd., *S. cymosum* var. *Smallii* (Britton) Fröd., *S. Smallii* (Britton) Ahles), $2n = 18$, is a conspicuous and consistent member of the vernal flora of granitic flat-rock communities of the upper and lower Piedmont of the Carolinas, Georgia, and eastern Alabama (McVaugh, 1943). Not totally restricted to granitic rock, *D. Smallii* also occurs in similar situations on sandstone outcrops and on sandy flats in Georgia, on the Cumberland Plateau of southeastern Tennessee, and in the mountainous regions of northeastern and central Alabama.

When *Diamorpha Smallii* was first discovered, apparently at Flat Rock, north of Camden, South Carolina, the type locality of *Sedum pusillum* Michaux, Nuttall confused plants of the two taxa, and, although the initial confusion was later clarified by Asa Gray (1876), the nomenclature of *Diamorpha* has been troublesome and further complicated by controversy over the acceptance of *Diamorpha* as a genus distinct from *Sedum*. Aspects of nomenclature have been clarified only recently by Wilbur (1964, 1977), who has applied the correct specific epithet, *Smallii*, to the single species. The name *Diamorpha Smallii* was originally proposed by Britton for a reputed second species (treated as a variety by Fröderström, 1935) based on immature plants that do not differ from other plants of *Diamorpha* of an equal developmental stage. See Wilbur's papers for the rationale behind the adoption of Britton's epithet, as well as for historical and other nomenclatural details.

The controversy over the distinctness of *Diamorpha* as a genus has undoubtedly stemmed from the overall morphological resemblance of *D. Smallii* and *Sedum pusillum*, as well as from their almost identical distribution and close ecological association. Moreover, McCormick (in McCormick & Platt, 1964) reported natural and artificial hybrids between *Diamorpha* and *Sedum* (presumably *S. pusillum*), but such hybrids have not been documented (cf. Sherwin & Wilbur, 1971).

Diamorpha has several distinctive morphological features, anatomical differences, and a chromosome number uncommon in *Sedum*, all of which substantiate generic status. *Diamorpha* is unique in the dehiscence of its follicles by flaplike abaxial valves (FIGURE 2, e), a type not found elsewhere in the Crassulaceae. The absence, except during developmental stages, of an adaxial suture line on the carpels and the coherence of the carpels at the base for about one-third their length further separate *Diamorpha* from *Sedum* in general, while its cucullate petals, its floral vascularization pattern (Sherwin & Wilbur, 1971), its usually deeper red pigmentation, and its different ecological niche separate *D. Smallii* from *S. pusillum* in particular.

As a winter annual rarely more than 10 cm. tall, *Diamorpha Smallii* has attracted the attention of several investigators (McCranie, McVaugh, Wiggs & Platt, McCormick & Platt, McCormick *et al.*, Sharitz, Baskin & Baskin, and Sharitz & McCormick) who have studied its life cycle and aspects of its ecology under both field and laboratory conditions to determine its specific adaptations to its unique habitat. As a result, *Diamorpha* is one of the biologically better-known taxa in the southeastern flora.

Seeds of *Diamorpha* germinate during late October and early November, a period of autumn rains and warm daytime temperatures (ca. 20° C.).

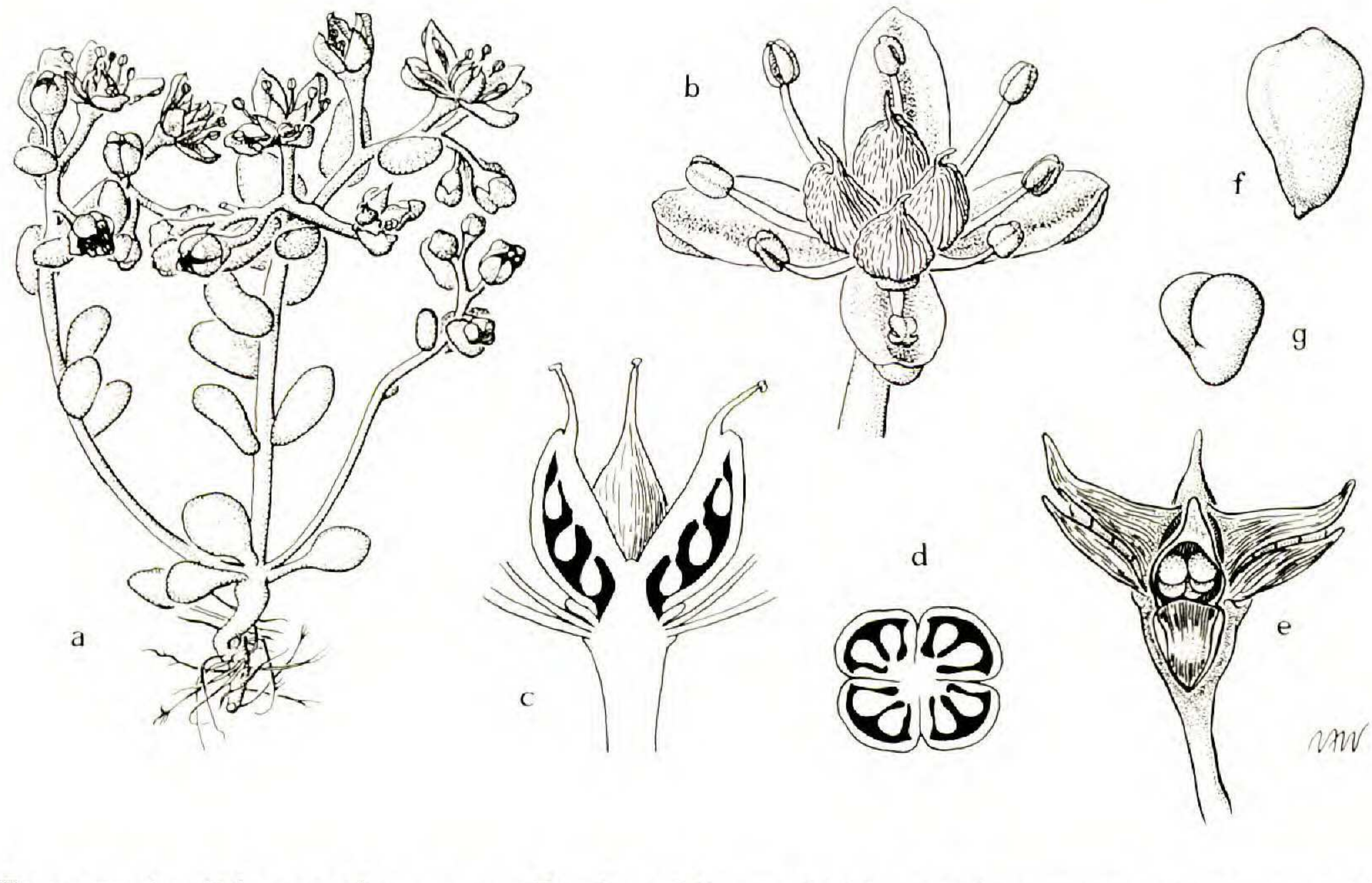

FIGURE 2. **Diamorpha.** a–g, *D. Smallii*: a, habit of flowering plant, × 1½; b, flower, × 8; c, longitudinal section through immature follicles (note nectaries at base of staminal filaments) showing pendulous ovules, × 10; d, cross section through four carpels of gynoecium in basal, syncarpous region, × 10; e, dehisced follicles, × 6; f, seed, × 30; g, embryo, × 25.

Although germination occurs readily under these conditions, seedling establishment is dependent on extensive secondary root development that, in turn, requires a substrate pH in the narrow range of 4.5 to 5. During establishment, plants can tolerate three or four weeks of total inundation or two to three weeks of desiccation before dying. If established, the plants assume a compact, rosette-like form, develop their characteristic deep red pigmentation, and become semidormant, with little further vegetative growth. Resistant to frost, the plants resume growth and initiate flower-bud primordia during late February. Branching and height of plants are determined at this time and are correlated with soil factors and competition, the latter of which is in turn related to population density. The inflorescences expand during March, and, depending upon locality, anthesis begins during late March and early April, reaching its peak toward the middle of April.

Details of the pollination ecology and breeding system have not been studied in great detail, but it has been noted that the four anthers opposite the sepals dehisce at the onset of anthesis, while the remaining four, which are held by the four petals, have a retarded dehiscence, shedding pollen toward the end of flowering. Bees and other unidentified insects have been observed visiting the flowers, and cross-pollination is to be expected.

Death of plants within a population begins by the middle of April, and by the middle of May most of them are dead. According to Wilbur, seed release from the mature follicles occurs by late spring and early summer, an observation contrary to Wiggs & Platt's finding that follicle dehiscence does not occur until late summer or fall, "until the continued action of moisture . . ." causes dehiscence, "a process requiring 2–5 months." According to Wiggs & Platt, retention of the seeds in the follicles above the outcrop surface over summer, during which time the seeds after-ripen, is an adaptive mechanism that protects the seeds from exposure to the high summer temperatures of the outcrop surfaces.

Observations of a series of populations of *Diamorpha* both in the field and in transplant studies on a simulated outcrop led McCormick & Platt to conclude that "*Diamorpha* is undergoing ecotypic variation," inasmuch as clinal phenological variation on a northeast to southwest gradient was detected and physiological differences between populations, related primarily to moisture gradients, were found. They summarized their findings and those of other investigators, saying that *Diamorpha* "has become adapted to the rigorous outcrop environment, both through drought evasion and drought tolerance. All stages of the life-cycle express unusual tolerances to extremely low or high moisture levels, and the entire life-cycle is adapted to make maximum use of favorable intensities and durations of moisture and to avoid periods of low moisture and high temperature."

The relationships of *Diamorpha* would appear at first glance to be with annual species of *Sedum*, yet certain evidence does not support this hypothesis. Fröderström (1935) allied *Diamorpha* (as *Sedum cymosum*) with *S. pusillum*, $2n = 8$, and *S. Nuttallianum* Raf., $2n = 10$, in his group 8, EPETEIUM AMERICANUM, and suggested affinities of this group with annual

European and Asiatic species. Baldwin (1940), like Berger (1930), maintained the generic status of *Diamorpha* and proposed that the genus might represent "amphidiploid results of fusion between representatives of the 4- and 5-chromosome tendencies" found within annual species of *Sedum*. However, Baldwin also suggested the possibilities of affinities with *Tillaea* of subfam. Crassuloideae.

The anatomical studies of floral vascularization conducted by Sherwin & Wilbur (1971) have shown, however, that Fröderström's group 8 is "highly heterogeneous." The differences between the taxa were seen by Britton & Rose to be sufficient to place the three species in different genera, viz., *Diamorpha, Tetrorum* (to include *Sedum pusillum*), and *Sedum*. The rather enigmatic and apparently isolated position of *Diamorpha* within the Crassulaceae was recognized by De Candolle (1828), who established the tribe Crassulaceae Anomalae to include *Diamorpha* and *Penthorum* L.

Torrey & Gray (1840) also grouped these two genera together in the crassulaceous tribe Diamorphae, a tribe maintained by Small (1933) for *Diamorpha* alone. It is probable that *Diamorpha* and the taxa to which it has been allied share superficial resemblances as a result of similar selection pressures and represent convergent groups within the Crassulaceae. In a family notorious for indistinct generic limits, the distinctiveness of *Diamorpha* is probably indicative of relatively great age.

Although no local uses have been recorded for *Diamorpha*, the plant has been important as a subject of continued biologic investigation. With the current knowledge of its life cycle, *Diamorpha Smallii* will undoubtedly continue to be valuable as an easily manipulated experimental plant.

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Subfam. CRASSULOIDEAE

3. **Crassula** Linnaeus, Sp. Pl. 1: 282. 1753; Gen. Pl. ed. 5. 136. 1754.

A diverse, polymorphic genus of diminutive [to large], prostrate to erect, aquatic or semi-aquatic [to xeromorphic], herbaceous [to subshrubby], branched [or unbranched], mostly succulent annuals, biennials [or monocarpic or polycarpic perennials], usually from fibrous roots [or occasionally from tuberous rhizomes], the plants of mosslike aspect, often rooting at the nodes. Leaves opposite, small and inconspicuous [or usually of moderate size, or rarely lacking and the internodes swollen], sessile [to distinctly petiolate], the internodes elongate [or often reduced in length and the leaves clustered and subrosulate, variously imbricate, or decussate and 4-ranked, the arrangement and shape of the leaves often giving the plants a *Lycopodium*-like or bizarrely geometric appearance], the leaf bases often connate and sheathing, the blades usually glabrous [or variously pubescent, sometimes with structural "windows" and subcuticular air bladders], with entire [or crenate or serrulate] margins. Flowers usually small, 3-, 4-, [or 5-, rarely 6–9-] merous, solitary [or sometimes clustered] in the axils of leaves [or terminal, usually arranged in terminal or axillary corymbose, thyrsoid, or subumbellate inflorescences, occasionally with bulbils or plantlets replacing the flowers]. Sepals small, greenish, shorter than the petals, ± erect [or flared], often connate at base. Petals small, [erect to] spreading, of various shapes, white [to pinkish or sometimes yellowish], greenish [or bluish], usually connate at base, [often with a small subapical mucro]. Stamens the same number as the petals, insertion hypogynous [or epipetalous on the shallow corolla tube], opposite the sepals, the filaments subulate to flattened or filiform, with ovate to oblong, basifixed anthers [sometimes with conspicuous connectives]. Gynoecium of 3–5 or rarely more, erect [or divergent], free or basally connate carpels, the carpels tapering [gradually] or abruptly to short and thick [or long and slender] styles, the stigmas small, terminal [or sometimes subapical]; ovaries unilocular, with 1, 2, or several to many ovules on placentae along the adaxial sutures. Fruits erect [or divergent] follicles, often with short stylar beaks, dehiscent along the adaxial sutures; seeds 1 to many, small, the embryo surrounded by endosperm. Base chromosome numbers 7, 8. (Including *Bulliarda* DC., *Hydrophila* House, *Tillaea* L., *Tillaeastrum* Britton.) LECTOTYPE SPECIES: *C. perfoliata* L.; see Hitchcock, Prop. Brit. Bot. 143. 1929. (Name from Latin, *crassus*, thickish, in reference to the thick, succulent leaves and stems of many of the species.) — CRASSULA.

A large, polymorphic, and ecologically diverse genus of nearly 300 species restricted in distribution, with the exception of members of one of the seven sections, to southern Arabia and to sub-Saharan Africa. The genus has its center of diversity, both in number of species and in morphological variation, in southern Africa. Unlike the species of sections restricted to Africa, members of sect. TILLAEOIDEAE DC. emend. Schönl., to which the following discussion is largely limited, are cosmopolitan in distribution, occurring on all continents except Antarctica. They are, moreover, the only representatives of the Crassulaceae in southern South America, New Zealand, and Australia.

In the southeastern United States sect. TILLAEOIDEAE is represented by *Crassula aquatica* (L.) Schönl. (*Tillaea aquatica* L., *T. simplex* Nutt., *Tillaeastrum aquaticum* (L.) Britton, *Hydrophila aquatica* House, *Bulliarda aquatica* (L.) DC., *Elatine tetrandra* Maxim.; including *Crassula Drummondii* (Torrey & Gray) Fedde), water pigmy, $2n = 42$, which has a documented distribution only in Louisiana. It may also occur in North Carolina,[6] and Hultén (1958) maps a locality for the species in the panhandle of Florida. Elsewhere in North America it occurs along the eastern

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[6] One specimen of *Crassula aquatica* in the Gray Herbarium has been considered an M. A. Curtis collection from North Carolina, but the collection data do not appear to date from Curtis's time. Radford, Ahles, & Bell (1968) do not report the species for the Carolinas.

seaboard from Quebec and the Canadian Maritime Provinces, southward into New England, New York, Delaware, and Maryland, and along the Pacific coast in Alaska, Washington, Oregon, and California. Fassett (1928, p. 106) suggests that in northeastern North America *C. aquatica* is probably a preglacial relic ". . . which has found estuarine conditions favorable for its existence." Inland, it has been collected from scattered, disjunct localities in the Canadian Northwest Territories (Mackenzie District), and in Minnesota, Nevada, Utah, Colorado, Wyoming, and New Mexico. Beyond North America *C. aquatica* has a wide, disjunct distribution in Asia and northern Europe.

A minute, glabrous annual or biennial with prostrate and nodally rooting to ascending or erect, usually branched stems, *Crassula aquatica* is tolerant of both fresh and brackish water. In the Northeast, it is most often found growing in estuarine situations or in the mud or wet sand of receding pond margins where it often forms mosslike mounds. In northern Louisiana, where the species has been found to be relatively common (Thomas, 1971), it is usually found growing in the moist depressions of animal or vehicle tracks in pastures and old fields. Due to its insignificant stature, it is probably often overlooked by collectors, and Thomas has classified the species as a "belly-plant." The small, usually four-merous, greenish or white flowers are solitary in the axils of the connate-sheathing leaf blades and are borne on short pedicels that usually elongate in fruit.

The variable pedicel length of flowering plants of *Crassula aquatica* and the tendency for the pedicels to elongate after anthesis have led both to confusion between species and to the recognition of a segregate species. Plants from Louisiana to Mexico and from California and Washington with the pedicels longer than the subtending leaves in fruiting specimens have been segregated as *C. Drummondii* (Torrey & Gray) Fedde (*Tillaea Drummondii* Torrey & Gray, *Tillaeastrum Drummondii* (Torrey & Gray) Britton, *Tillaea aquatica* var. *Drummondii* (Torrey & Gray) Jepson), but such segregation is artificial when the range of pedical length within *C. aquatica* is considered, and most authors now include *C. Drummondii* within *C. aquatica*. Other plants from Prince Edward Island with the flowers distinctly pedicellate were originally confused with *C. Vaillantii* (Willd.) Roth, a species of Central Europe and northern Africa.

While there has been confusion about the other species of *Crassula* sect. TILLAEOIDEAE that occur in North America, it appears that only two additional ones have been found in the United States. Britton & Rose (1905) included two others as occurring in Mexico. *Crassula erecta* (Hooker & Arnott) Berger (*Tillaea erecta* Hooker & Arnott, *C. minima* Miers), sand pigmy, $2n$ = ca. 16, ca. 20–25, a species of dry, open locations, is native from southern Oregon southward, through California and Arizona, into Baja California; it also occurs disjunctly in Chile. *Crassula muscosa* (L.) Roth (*Tillaea muscosa* L.), a European species, has been reported from Amador and Calaveras counties, California. It has apparently become naturalized in the Great Valley of California and in an area in the southern North Coast Ranges (Clausen, 1975, p. 608).

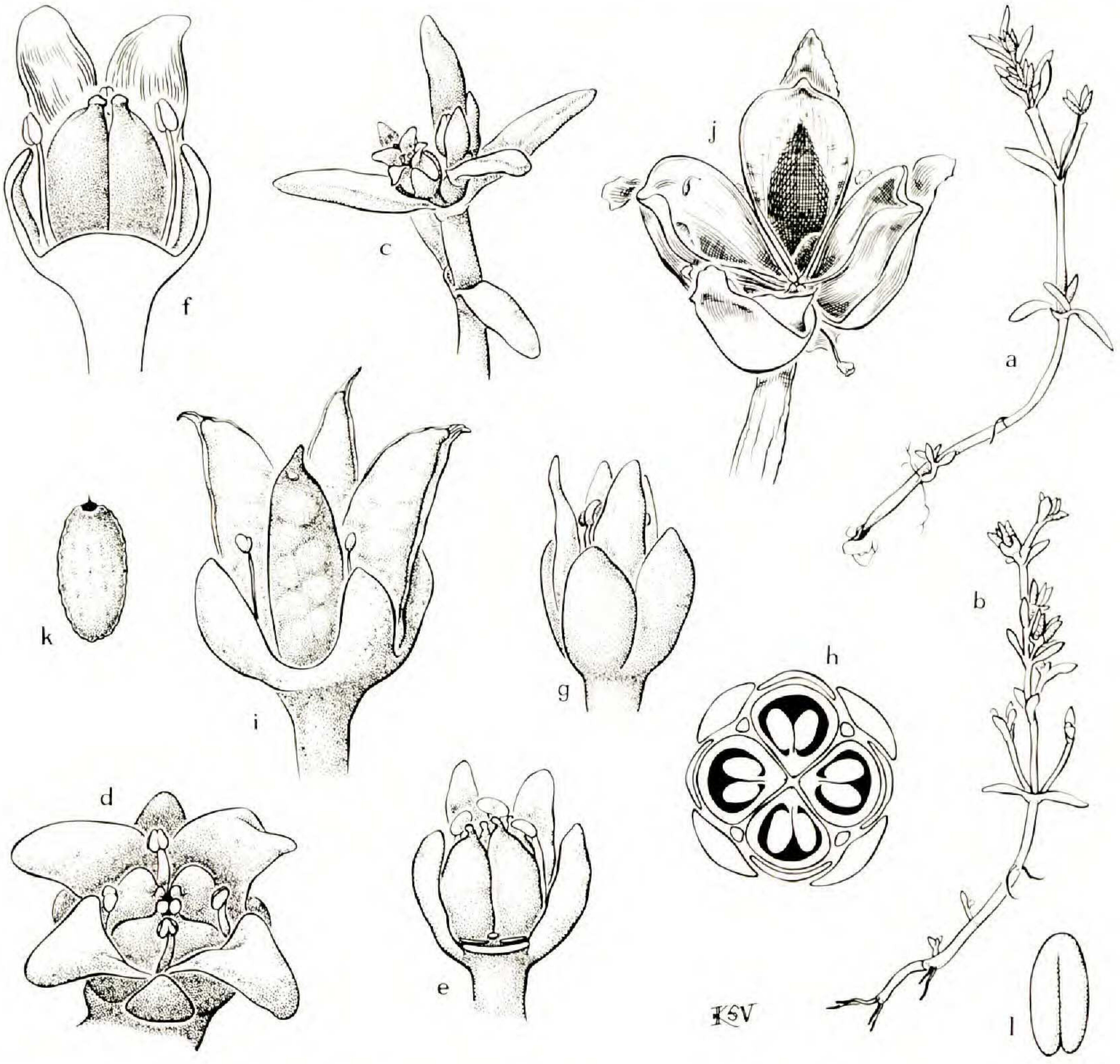

FIGURE 3. **Crassula.** a–l, *C. aquatica*: a, b, two plants, × 3; c, tip of shoot with axillary flower, × 6; d, flower, × 25; e, flower with petals and one stamen removed (note nectaries at base of carpels), × 25; f, longitudinal section through flower, two carpels removed, × 25; g, flower after anthesis, × 25; h, cross section through flower after anthesis, × 25; i, immature follicles, × 25; j, dehisced follicles, × 20; k, seed, × 50; l, embryo, × 50.

The union of *Tillaea* L. with *Crassula* has not been universally accepted. Authors of many floristic works have retained *Tillaea,* and some have divided *Tillaea* itself into small genera. Britton (1903), for example, established *Tillaeastrum* for species (*C. aquatica*) with solitary flowers and several-ovuled carpels, retaining *Tillaea,* sensu stricto, for species with clustered flowers and with carpels containing one or two ovules (e.g., *C. erecta*). However, as defined by Schönland, sect. TILLAEOIDEAE, comprising several groups or series,[7] combines these and other species that had otherwise been treated as segregate genera or sections of *Crassula.* Segregate taxa have been based primarily on the number of floral parts, ovule number, and nectar-scale shape. But, as Schönland (1916, p. 42) notes, these characters are "useless for generic distinction, as they may

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[7] Schönland gave no rank to his subdivisions of sect. TILLAEOIDEAE; Jacobsen (1970) has designated them as series.

separate species which are otherwise closely allied and moreover they are sometimes not constant in one and the same species."

As a group, species of sect. TILLAEOIDEAE consist of small, morphologically variable, annual, biennial, or perennial plants adapted to wet soils (some are true aquatics), while others are decided xerophytes. The petals, which are usually spreading at anthesis, never form an urceolate corolla (a condition Schönland considers to be a xerophytic adaptation), and they lack the subapical mucro characteristic of *Crassula* sensu stricto. Despite these deviations, Schönland states that "no sharp line can be drawn between the Tillaeoideae and other sections of *Crassula*." He suggested further that species of sect. TILLAEOIDEAE are the least derived species of *Crassula* and that a great age for the section could be deduced from the widespread distribution of its species. Fröderström (1930, 1931) went so far as to suggest that *Tillaea*, which he maintained as a genus, was ancestral to the entire Crassulaceae. But Berger (1930) cautioned that species of the TILLAEOIDEAE are probably highly derived, reduced forms, an opinion shared by Uhl (1948), who suggested that the wide distribution of the section (and of individual species) is attributable to very efficient seed dispersal. Quimby (1971), who studied the floral anatomy of *C. aquatica*, also suggests that *Tillaea*, as a genus, could be considered a reduced form of *Crassula*.

Among other genera of the Crassulaceae, Schönland favored a possible origin of *Crassula* from the usually obdiplostemonous genus *Sedum*. Some species of *Sedum* sect. EMPETEIUM Boiss. (*Sedum* sect. *Procrassula* (Griseb.) Schönl., pro parte, *Procrassula* Griseb.) are haplostemonous, and, except for their alternate leaves, are suggestive of *Crassula*. The idea of an origin of *Crassula* from *Sedum* is given some support by Mauritzon (1933), who, on the basis of embryological data, concluded that *Crassula* (and *Tillaea*) is evolutionarily younger than *Sedum*. Quimby (1971) states that floral anatomical evidence, i.e., the single whorl of stamens and the lack of or small size of certain carpel traces, also supports this hypothesis.

Interspecific hybrids in *Crassula* appear to be very rare. However, the presence of an extensive polyploid series suggests reticulate relationships among the species. That sect. TILLAEOIDEAE has a base chromosome number of $x = 8$, as was suggested by Baldwin (1936), has been confirmed by the recent investigations of Merxmüller *et al.* (1971) and Friedrich (1973); yet the one discordant count for the section is that of $2n = 42$ for *C. aquatica*. Otherwise, somatic numbers range from 16 to ca. 128, all multiples of eight. Most other sections of *Crassula* have a base chromosome number of 7 (from the diploid to the decaploid level), but some sections share both base numbers. As noted by Uhl (1956), "the significance of the different basic chromosome numbers with respect to taxonomy is not yet known," but Friedrich asserts that "polymorphic aggregates, e.g. the *Crassula lycopodioides* complex, are extremely heterogeneous with regard to their caryological conditions. It appears that different species have been united often unjustifiedly in such cases."

The ease by which plants of *Crassula* species are propagated vegetatively has enhanced the use of these succulents as house plants. *Crassula lycopodioides* Lam., $2n = 16, 32, 48, 64, 96$ (sect. TILLAEOIDEAE series *Lycopodioides* Schönl.) and *C. pyramidalis* Thunberg, $2n = 14, 28$ (sect. PYRAMIDELLA Harvey), both of South Africa, are but two of the many species of *Crassula* available at florist shops. Perhaps the best known species is *C. argentea* Thunberg (*C. portulacea* Lam.), $2n = 42, 56$ (sect. STELLATAE Schönl.), also of South Africa and commonly known as the jade tree or Chinese rubber tree. Widely grown as a house plant, it is sometimes grown out-of-doors in warmer temperate regions as a perennial ornamental. The nomenclature and taxonomy of these and other species, however, is often confused and open to dispute, a situation due in large measure to the difficulties of preparing adequate, identifiable herbarium specimens of succulent plants.

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Subfam. KALANCHOIDEAE Berger

4. **Kalanchoë** Adanson, Fam. Pl. 2: 248. 1763.

Glabrous or pubescent, [monocarpic or] polycarpic perennial herbs, subshrubs, or shrubs, often of twining or rambling habit, the majority terrestrial from fibrous roots [or some epiphytic], many gemmiparous and viviparous. Leaves opposite and decussate or in whorls of 3, simple or occasionally pinnately compound, the simple leaves sessile to petiolate, the bases of the blades or the petioles often amplexicaul; blades ± succulent, flattened to ± cylindrical with entire, crenate, dentate, or pinnatisect margins, often with adventitious buds in the crenations of the leaf margins producing plantlets. Flowers perfect, usually numerous, erect to pendent in terminal or sometimes axillary, bracteate, paniculate or cymose inflorescences, sometimes with adventitious buds in the axils of the bracts; insertion of the calyx and corolla hypogynous. Sepals 4, weakly to strongly connate, forming a cylindrical, often inflated calyx tube, the 4 free lobes shorter to longer than the tube. Petals 4, violet through red and pink to white, yellow, or greenish, connate for most of their length, forming a cylindrical to ± campanulate or ± urceolate, usually 4-angled corolla tube, the tube sometimes basally constricted over the gynoecium and the 4 free lobes spreading to recurved. Stamens 8 [or rarely 4], epipetalous in 2 whorls of 4, usually exserted; filaments slender, tapering to the basifixed, yellowish anthers. Gynoecium 4-carpellate, the erect or divergent carpels connate at least basally; carpels constricted above the ovaries into slender, usually included styles, the stigmas small, often poorly or not differentiated; ovaries unilocular with numerous anatropous ovules on placentae along the adaxial sutures. Fruits erect or divergent, papery to coriaceous follicles dehiscent along the adaxial sutures; seeds numerous, very small, usually ± oblong and with rugose or wrinkled seed coats; embryo straight, small, embedded in endosperm, the megagametophyte of the Polygonum type. Base chromosome numbers 17, 18, 20. (*Vercia* Andrews, including *Bryophyllum* Salisbury, *Kitchingia* Baker.) TYPE SPECIES: *K. laciniata* (L.) A. P. de Candolle. (Name apparently derived from the Chinese name for one of the species; cf. W. H. Harvey in Harvey & Sonder, Fl. Capensis **2**: 327–380. 1894.) — KALANCHOË, BRYOPHYLLUM.

Approximately 125 species in three sections, the large majority endemic to Madagascar, others indigenous to Africa and Socotra, one or two widely distributed in both the Old and New World tropics. In the southeastern United States eight species have been reported as naturalized, all in southern Florida. Lakela & Craighead (1965) included three species in their checklist, while Long & Lakela (1971) considered six. Recent collections by Brumbach on Captiva and Sanibel islands, Lee County, indicate that one or two additional species have become established, primarily on the latter island.

Six of the eight species occurring in our area belong to sect. BRYOPHYLLUM (Salisb.) Boiteau & Mannoni (*Bryophyllum* Salisb.), a section characterized by opposite or usually whorled leaves, pendent flowers with tubular, often inflated calyces with the lobes shorter to longer than the tube, the corollas often constricted basally with the stamens inserted near the base, and the carpels erect. Plants of many species of this section produce plantlets in the crenations of the leaves. The remaining four naturalized species are members of sect. KALANCHOË and are characterized by opposite leaves, erect flowers with the calyx of free or basally united sepals, unconstricted corollas with the stamens inserted at or near the middle, and erect and contiguous carpels. In species of sect. KALANCHOË, plantlet production is apparently restricted to cut or injured surfaces. The third section, KITCHINGIA (Baker) Baillon (*Kitchingia* Baker), composed of plants with opposite leaves, pendent to nodding flowers with the calyx lobes about as long as the calyx tube, basally constricted corollas with the stamens inserted near or above the middle, and divergent carpels, is not known to be represented in the southeastern United States.

Of the species belonging to sect. BRYOPHYLLUM, *Kalanchoë pinnata* (Lam.) Persoon (*Cotyledon pinnata* Lam., *Bryophyllum calycinum* Salisb., *B. pinnatum* (Lam.) Kurz, *Sedum madagascaricum* Clus.), $2n = 36$, 38(?), 40, is undoubtedly the most widely naturalized species in our area. Often forming dense colonies in waste and disturbed areas, it has been reported from Palm Beach, Hendry, Lee, Collier, Monroe, and Dade counties. Plants of *K. pinnata*, which can reach two meters in height, are easily recognized by their hollow stems and their large paniculate inflorescences of flowers with papery, inflated, greenish white to pinkish or reddish calyx tubes 2.5–4 cm. long. Initially producing simple leaves with crenate margins, mature plants develop pinnately compound leaves with three or five leaflets. Both types of leaf produce plantlets in the crenations of the margins, and it is by this vegetative means that extensive colonies of plants have developed. Widely distributed throughout the tropics and subtropics of both hemispheres, it is probable that much of the wide range of *K. pinnata*, the nativity of which is uncertain, is due to the activities of man.

Flowers of *Kalanchoë Gastonis-Bonnieri* Hamet & Perrier, $2n = 34$, are similar to those of *K. pinnata* but are smaller, and the calyces are less inflated. The corollas, which extend beyond the calyx tubes, are either yellowish green or reddish, but apparently only the latter color form is represented in our flora. The plants produce large, consistently simple, lanceolate to spatulate, whitish to purplish leaves, sinuate to crenate at the margins. Native to Madagascar, *K. Gastonis-Bonnieri* has become well established on Sanibel Island, Lee County, Florida.

Kalanchoë tubiflora (Harvey) R. Hamet (*Bryophyllum tubiflorum* Harvey, *K. delagoënse* Eckl. & Zeyh., *B. delagoënse* (Eckl. & Zeyh.) H. Schinz; including *K. verticillata* Scott-Elliot, *B. verticillatum* (Scott-Elliot) Berger), $2n = 34, 40, 68$, has also been reported as naturalized in several areas of Florida in Martin, Palm Beach, Lee, and Collier counties, where it has been noted growing in waste places and on shell mounds. Widely grown as a pot plant, *K. tubiflora* is characterized by its distinctive violet-brown-spotted, more-or-less cylindrical leaves that are shallowly grooved on the adaxial surface and notched at the apex where bulbiferous spurs produce an abundance of plantlets. The flowers, which are notable for their relatively short calyces but long, pinkish to red corollas with spreading lobes, are produced in cymose corymbose inflorescences. Native to Madagascar, *K. tubiflora* is probably indigenous to areas of South Africa as well.

Also well known as a pot plant, *Kalanchoë Daigremontiana* Hamet & Perrier (*Bryophyllum Daigremontianum* (Hamet & Perrier) Berger), $2n = 34$, has become established in Palm Beach County and on Sanibel Island, Lee County. It has also been collected at Key West and may be naturalized elsewhere in the Florida Keys. The erect, glabrous, robust plants of this species, which is native to Madagascar, attain one meter in height and produce decussate, petiolate leaves with large, succulent blades that are spotted or blotched reddish brown beneath and are often ± auriculate at base. Abundant plantlets are produced by adventitious buds in the notches along the crenate to serrate margins. The pendent, lavender flowers are similar to those of *K. tubiflora*.

Kalanchoë laxiflora Baker (*Kitchingia laxiflora* Baker, *Bryophyllum crenatum* Baker, *Kalanchoë Tieghemi* Hamet, *K. crenata* Hamet, not Haw.), $2n = 34$, also native to Madagascar, has been reported as naturalized in waste places in Collier, Monroe, and Dade counties. A glabrous perennial to 5 dm., *K. laxiflora* is easily distinguished by its decussate, petiolate leaves with variable ovate to pandurate blades with crenate margins and ± auriculate bases. Like the other species of sect. BRYO-

PHYLLUM, plants of *K. laxiflora* produce plantlets in the crenations of the leaves. The flowers, with short, ± inflated calyces and relatively long, red to rosy- or yellowish-orange corollas, are produced in branched, paniculate inflorescences.

Unlike other naturalized species of sect. BRYOPHYLLUM, plants of *Kalanchoë Fedtschenkoi* Hamet & Perrier, $2n = 34$, develop into low, dense, many-branched shrubs with procumbent stems that eventually turn upward. Long, stiff adventitious roots are produced along the procumbent parts of the stems, and the short-petiolate, decussate leaves are closely spaced. The bluish green blades are ovate with rounded apices, and the crenate margins are brownish tinged in the crenations. The flowers, produced in terminal dichasial inflorescences, are brownish pink. Another native of Madagascar, *K. Fedtschenkoi* is known to be established in our area only on Sanibel Island, Lee County, Florida.

Of the two species of sect. KALANCHOË that are naturalized in our area, *K. marmorata* Baker (*K. grandiflora* A. Rich., not Wight & Arn., *K. somaliensis* Baker, *K. macrantha* Baker), $2n = 34$, is perhaps the most distinctive. A glabrous shrub usually branched from the base and with erect or sometimes procumbent stems, plants of *K. marmorata* are easily recognized by their sessile to shortly petiolate leaves with undulating to crenate margins that are green to plum colored and often brownish spotted on both surfaces. The erect flowers, borne in corymbose cymes, are characterized by long, white corolla tubes, 8–10 cm. long, terminated by short, deltoid lobes. Native to Ethiopia and Somalia, it is reported by Long & Lakela (1971) to be established in hammocks and disturbed sites in southern Florida, where it often forms extensive colonies.

Kalanchoë crenata (Andr.) Haw. (*Veria crenata* Andr., *K. integra* (Medic.) O. Kuntze var. *crenata* (Andr.) Cufodontis), a shrub with long-petiolate, elongate-lanceolate leaves with doubly dentate margins and yellow flowers produced in glandular-pubescent inflorescences, is the second species of sect. KALANCHOË naturalized in Florida. Long & Lakela (1971) list it as occurring in disturbed sites and hammocks in South Florida, and I have seen a specimen collected in 1973 from Sanibel Island, Lee County. Considerable taxonomic and nomenclatural confusion apparently surround *K. crenata*, and plants of this and closely allied taxa have been given varying taxonomic recognition (cf. Bailey *et al.*, 1976; Jacobsen, 1960, 1970; Baldwin, 1938; and Long & Lakela, 1971). As a result, various names, including *K. laciniata* (L.) DC., have been applied to our plant, apparently a South African native, and taxonomic and nomenclatural aspects need clarification. Baldwin (1938) found $2n = 34$ and $2n = 68$ for plants of this complex supposedly corresponding to *K. laciniata*, sensu lato, and $2n = 102$ for plants determined as *K. crenata*.

Much of the taxonomic attention given *Kalanchoë* has centered around its generic boundaries and the validity and status of *Bryophyllum* and *Kitchingia*. Many botanists have followed Baillon (1885), who included *Kitchingia* as a section of *Kalanchoë*, and Hamet (1907, 1908), who incorporated both *Bryophyllum* and *Kitchingia* within *Kalanchoë* as the sole genus of subfam. Kalanchoideae. Hamet placed the species in 14 groups of undesignated rank, while Boiteau & Mannoni (1947–1949) arranged the species in three sections (and numerous subsections) that reflect the originally proposed generic boundaries.

Those who have maintained or supported the maintenance of three genera have included Berger (1930), and Tillson (1940), who offered anatomical evidence in support of her position. Tillson found that in all three taxa ". . . the four petal traces are adnate to the corresponding antepetalous stamen trace as it leaves the floral axis." Despite the level of stamen insertion, however, consistent differences in the level of divergence of the two traces were noted. In *Bryophyllum* the traces separate below the level of corolla insertion, while in both *Kalanchoë*, sensu stricto, and *Kitchingia* separation occurs at some level in the corolla.

However, the intermediate morphology of several species originally indicated that the three genera should be treated as one, and this position has been supported by interpretations given both embryological (Mauritzon, 1933) and cytological (Baldwin, 1938) data. More recently, Friedmann (1971), who has surveyed the chromosome numbers of numerous Madagascan kalanchoës, has cautioned that additional cytological data together with geographical evidence may indicate that two genera, *Bryophyllum* (including *Kitchingia*) and *Kalanchoë*, are justified. It is obvious that additional evidence will be required to validate either the continued use of one genus or of two or three genera, and to gain unanimity among botanists. The choice made here to consider subfam. Kalanchoideae as consisting only of *Kalanchoë*, itself comprising three sections, is provisional — a choice of convenience that preserves the identity of the three taxa, yet reflects what are very close and undoubtedly reticulate relationships between them.

Chromosomes of *Kalanchoë* are small, yet chromosomal morphology is generally discernible and may be variable within a species complement; heterochromatic fragments have also been observed in several species. Chromosome numbers have been reported to range between $2n = 34$ and $2n =$ ca. 500, but most species are either diploid with $2n = 34$ or 36, or tetraploid with $2n = 68$ or 72. *Kalanchoë crenata* is probably a hexaploid with $2n = 102$; *K. Grandidieri* Baillon, $2n =$ ca. 140, is likely an octoploid; and *K. Faustii* Font Quer is a decaploid with $2n = 170$. Multivalent or secondary associations during meiosis apparently are uncommon.

While the majority of species of sect. KALANCHOË have chromosome numbers based on 18, and most of those of sects. BRYOPHYLLUM and KITCHINGIA are based on 17, there is incomplete coincidence between base chromosome number and sectional lines. Baldwin (1938) proposed that, of the possible base numbers for the genus, viz. 17, 18, 20, the primary number is 17. His suggestion was based on the hypothesis that *Kalanchoë* had an origin involving members of subfams. Crassuloideae and Cotyledonoideae Berger where base chromosome numbers of 7 or 8 and 9, respectively, were suspected. Both subfamilies are well represented in the geographical area where *Kalanchoë* is indigenous.

Although the prevalent diploid number found in *Kalanchoë* is 34, a number based on 17, Uhl (1948) proposed that the Kalanchoideae may have had an origin completely within the Cotyledonoideae, and that, as a result, the primary base chromosome number for *Kalanchoë* is 18. Uhl's proposal is strengthened if members of *Crassula* sect. TILLAEOIDEAE are considered to be derived members of that genus. This interpretation requires that, of the two possible base numbers for the Crassuloideae, 7 or 8, seven be taken as the primary number, thereby excluding the great majority of taxa of the Crassuloideae except species of sect. TILLAEOIDEAE as possible ancestors of the Kalanchoideae. Based on morphology alone, this hypothesis seems doubtful, while the separation between the Kalanchoideae and Cotyledonoideae is based solely on four-merous flowers in the former and five-merous flowers in the latter subfamily.

The production of plantlets along the margins of leaves by species of *Kalanchoë* sect. BRYOPHYLLUM has attracted the attention of numerous investigators. Stoudt summarized the studies prior to 1938 and pointed out that for all the Crassulaceae investigated, a residual meristem or a secondary "cicatrice" meristem formed from parenchyma cells produces root primordia endogenously and shoot primordia exogenously. Differences in plantlet formation consist of the presence or absence of residual meristems, the location of the meristematic activity, the conditions under which meristematic activity and/or growth of primordia are initiated, and, if residual meristems are present, the degree to which primordia are developed on mature plants. In species of sect. BRYOPHYLLUM, meristematic activity and subsequent growth of plantlets can occur on either attached or detached leaves. In species of sect. KALANCHOË, growth of a new plantlet is apparently induced only when leaves are detached. Moreover, the residual meristematic region in species of sect. KALANCHOË is at the base of the leaf or petiole, not in the crenations of leaf margins.

Numerous studies have attempted to determine the factors that trigger or inhibit the activity of the meristems and the growth and development of the primordia, which in species of *Kalanchoë* are well differentiated when the leaf on which they occur is still immature. The literature concerning this aspect of plantlet production is large, and no attempt has been made to summarize it here. It appears, however, that there are conflicts and contradictions in the literature, and it would be helpful if a plant physiologist could summarize this knowledge; to this end, numerous references are included below.

Because of the ease of propagation of plantlets and the resulting availability of clonal populations, plants of *Kalanchoë* have proven to be apt subjects in experimental studies. Much information concerning the genus has accumulated and is scattered in the physiological literature. For example, it has been determined that *Kalanchoë Blossfeldiana* Poelln. is a typical short-day plant, while *K. crenata, K. tubiflora,* and *K. Daigremontiana* are long-short-day plants. Van de Pol (1972) has summarized available information concerning floral induction and flowering in *Kalanchoë*, and his paper should be consulted for numerous pertinent references of a physiological nature not cited here.

In another study, Groner (1974) has reported that parent plants of *Kalanchoë Daigremontiana* produce a water-soluble allelopathic agent that greatly retards growth (as well as eliciting a syndrome of related characteristics) in daughter plantlets that become rooted within the radius of the parent plant's root system. Groner suggests that this influence is an adaptation for the control of both population size and density. In Madagascar, where the species is native, plantlet production is increased during the rainy season, when it is probable that the plantlets are detached and washed to new areas for establishment. An allelopathic effect was also observed on germination and growth of plants of several other species of monocots and dicots, while others were unaffected, and Groner (1974, 1975) suggests that the allelopathic compound is a unique glycoside, bryophyllosid, recently characterized by Karsten (1965).

No information concerning the breeding system or pollination ecology of *Kalanchoë* has been located, except for the suggestion that flowers of *K. pinnata* are adapted for hummingbird pollination (Knuth, 1908). However, Craft (1942) has described the occurrence of extrafloral nectaries on the uppermost leaves and lowermost floral bracts in *K. pinnata.* These "nectaries" (glandular tissue lying in pitted areas on the lamina) appear and produce droplets high in glucose content only when the plants are in flower.

Several hybrids have been reported in *Kalanchoë*, but all references located refer to hybrids that have arisen either in cultivation or through intentional crosses. A triploid hybrid, $2n = 51$, between *K. Daigremontiana* and *K. tubiflora*, both of sect. BRYOPHYLLUM, has been reported by Baldwin (1949) and Warden (1958). Displaying a morphology intermediate between the parental species, the hybrid is apparently well established in American horticulture and is sometimes referred to as *K.* × *hybrida* Hort. Another hybrid has involved *K. Daigremontiana* as the pollen parent and *K. pinnata* as the seed parent, while the intersectional hybrid, *K. Daigremontiana* × *K. Blossfeldiana*, and its reciprocal, have been produced by Resende (1956). Maintaining two genera for the parental species, Resende gave the hybrid group the name × *Bryokalanchoë lisbonensis*, apparently an invalid one lacking a Latin description. Resende's observations on these sterile hybrids indicate that "the capacity to form pseudobulbs is recessive and that SD [short-day] is dominant over LSD [long-short-day]."

Aside from their usefulness in experimental studies, several species of *Kalanchoë* are of economic importance as pot plants. Within recent years numerous cultivars of *K. Blossfeldiana* have been selected and marketed as winter-blooming house plants, and most florist shops offer this species for sale during the Christmas season and into the spring months. Many other species are widely grown by fanciers of succulent plants and may occasionally be found for sale in florist shops.

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